# THE ALIMENTARY CANAL OF PHILAENUS LEUCOPHTHALMUS L.*

RODNEY CECIL,
U. S. Bureau of Entomology.

## INTRODUCTION.

A study of the alimentary canal of *Philaenus leucophthalmus* L. was undertaken to determine the gross and histological structure of the tract and the source of the "spittle" with which the nymphs of this well known species of cercopid cover themselves.

This work was begun as a study in internal morphology, under the direction of Dr. C. H. Kennedy at the Ohio State University. Owing to the complexity of the alimentary canal, the work was not completed in the allotted time but has been continued as time permitted. The assistance and suggestions of Dr. Kennedy have been a great aid in the progress of the study.

## METHODS.

Various methods of gross dissection were used at first without success. Serial sections were then prepared and drawings were made of each in an effort to reconstruct the complex diverticular region of the canal. Owing to the numerous loops and convolutions of the structures involved, this method also was unsuccessful. In fact, the completion of the study was almost despaired of until the following method for dissecting was discovered:

The specimen to be dissected was placed in a vial and given an anesthetic of ether or chloroform. As soon as the insect became quiet, it was removed from the vial to a dissecting dish which had a layer of blackened paraffin in the bottom. The specimen was then placed dorsal side up in normal position and its legs imbedded in the paraffin by melting the paraffin around them with a hot needle. When the paraffin cooled, the specimen was held securely by its legs. The insect was then covered with lukewarm normal saline solution. The usual method of gross dissection was followed with as much speed

*Contribution No. 100 from the Department of Zoology and Entomology, Ohio State University.

and caution as possible. The advantage of dissecting a live specimen lies in the transparency of live tissue. The convolutions of the stomach in the folds of the diverticula can be seen through the transparent covering of connective tissue on a living specimen. This can not be done on a dead specimen since dead tissue is opaque.

For the histological study the best sections were secured by the following method:

Nymphs and adults, collected just after molting, were killed by placing them in hot water at 70° C. for 3 minutes, fixed in Kahle's solution for 24 hours, and stored in 70 per cent alcohol. For study, after the usual preparation they were imbedded in paraffin, cut into sections 10 microns thick, mounted, and stained in hematoxylin and eosin.

## Gross Anatomy of the Alimentary Canal.

The Cercopidæ secure their food by piercing the host plant with the modified mandibles and maxillæ, which rest in the grooved labium, and then pumping the liquid or sap up the tube from the rostrum by means of the pharynx.

The ducts of the salivary glands empty into the mouth cavity just anterior to the pharynx. There are two pairs of salivary glands which lie parallel to the oesophagus, (Fig. 1). One pair is above and laterad and the other ventrad and laterad of the oesophagus. The upper two are almost cylindrical whereas the lower two are club-shaped and taper posteriorly. Their length is approximately the same as that of the oesophagus. Each gland has a duct that leads anteriorly into the head where the duct of the lower gland fuses with the corresponding duct from the upper gland. The two ducts coil in the head region and then empty into the mouth cavity.

The pharynx is an enlargement of the fore intestine. It is slightly diamond shaped, is situated in the head posterior to the brain, and operates as a pump by means of numerous pharyngeal muscles. Food passes from the pharynx into the oesophagus.

The oesophagus is a long tube connecting the pharynx and oesophageal valve. It decreases in size posteriorly to the anterior region of the mesothorax, then enlarges slightly. This enlargement may indicate the remains of a crop. The oesophagus decreases in size in the metathoracic region, where the oesophageal valve is located. See Plate II, fig. 6.

The oesophageal valve is well developed structurally in this species and marks the division between the fore intestine and the mid-intestine. Before the first and second divisions of the stomach are "teased" apart the location of the oesophageal valve is often not apparent.

The mid-intestine begins at the oesophageal valve and ends at the point where the Malpighian tubes enter the canal. The anterior end of the mid-intestine is composed of two large pouch-like structures.

From a dorsal view, the first pouch or anterior diverticulum is located to the right and is slightly kidney shaped. Adjoining this pouch, slightly posteriorly and to the left, is a second pouch or posterior diverticulum of approximately the same size but less muscular.

The heavy walled anterior diverticulum retains its approximate position in a dead specimen, but the posterior diverticulum usually collapses and folds posteriorly, (Plate II, fig. 6). When the muscles and tissue connecting the two pouches are severed it is seen that the anterior and posterior diverticula are connected as shown in Plate I, Figure 2. The posterior diverticulum tapers posteriorly from the first to the second abdominal segments, then proceeds as a small, thin walled, light pink gut that continues ventrally and posteriorly to the 5th or 6th abdominal segment. The gut is constricted at this point and then immediately enlarges to twice its former size, (Figs. 1 and 13). Besides being of much larger size the gut is now yellow and opaque, and is full of irregular shaped objects. This yellow portion of the gut is easily seen through the semitransparent body wall of the nymph at the sixth or seventh segment. The gut continues to loop cross-wise of the body to the seventh abdominal segment; then turns and proceeds anteriorly, the yellow colored granules being present to about the third abdominal segment, where they gradually disappear. This condition exists in both nymphs and adults. As the granules decrease in number the gut assumes the same size and color as that portion which is anterior to the constriction. After many loops this portion of the stomach appears to enter the anterior diverticulum, at various points as shown in Plate I, Figures 2, 3, 4 and 5. The portion just described, with the constriction, has been described by Gadd (2)* as two blind caeca and the constriction given as the point where the two caeca had fused. This investigator was confused because the gut just described apparently entered the first pouch and because a second gut from this pouch proceeded to the anus. What became of the gut that entered the pouch and where the one leaving it came from was a mystery in this study until the method of gross dissection, previously described, was discovered.

The posterior portion of the mid-gut may also disappear under a fold of the wall of the posterior diverticulum as shown in Plate II, Figure 6, but is usually enfolded only by the anterior diverticulum as shown in the simplified diagrammatic drawings of Plate I, Figures 3, 4 and 5. The posterior mid-gut usually ascends in a fold of the diverticulum with few loops, to a point laterad of the oesophageal valve where the two pairs of Malpighian tubes are attached. There is an enlargement of the gut at this point which may be the location of a pyloric valve, though no valve was recognized in cross or longitudinal sections from this region. From this point the descending gut is the hind intestine.

The hind intestine extends from the point of attachment of the Malpighian tubules to the anus. The anterior portion makes several loops as it zigzags posteriorly in the fold of the wall of the anterior diverticulum before it appears at the posterior tip, (Plate I, Fig. 2).

*Number in parenthesis refers to Literature cited, page 127.

This intestine loops crosswise of the body and lies near the dorsal body wall, (Plate I, Fig. 1). The hind intestine is of uniform size to about the eighth abdominal segment, where it enlarges to form the rectum.

The Malpighian tubes are four in number and join the hind intestine as shown in Plate I, Figure 2.

The ascending anterior portions of the Malpighian tubes become small, thin-walled, and symmetrical just before they are enfolded by the anterior diverticulum and remain so to the point of attachment. Their posterior portions are relatively large, irregular in shape and have the appearance of a string of beads. This characteristic bead shape of the Malpighian tubes is due to the size and shape of the cells, (Plate II, Figure 16).

The Malpighian tubules lie next to the dorsal body wall and make crosswise loops similar to those of the descending hind intestine. They extend posteriorly to the seventh or eighth abdominal segment, and terminate with blind ends.

The rectum is a heavy walled, straight tube, that ends at the external anal opening, (Plate I, Fig. 1).

## Histology of the Alimentary Canal.

The fore intestine from a histological point of view is not unusual. It is lined with a thin layer of chitin or intima which is extremely thin in the region of the oesophageal valve. The hypodermal cells of the oesophagus are well developed. In the anterior portion the cells have relatively large nuclei, are crowded, and assume a columnar shape. The cells of the middle to posterior portion of the oesophagus are cuboid in shape with rather elongated nuclei. In the oesophageal valve region the cells are much crowded, very long, with the nuclei as wide as the cell. (See Plate II, Fig. 6.)

The large salivary glands that are located parallel to the oesophagus have a peculiar cell structure. The upper pair have large cells with numerous irregular shaped lumens that are perhaps portions of connecting ducts, (Fig. 11). The lower pair of salivary glands is much larger than the upper pair and the cell arrangement gives them the appearance of rosettes. In cross section (Fig. 12) there is seen a common central duct with cells arranged around the duct. A chitinous lined duct results from the union of the ducts from the upper and lower glands, and this coils in the head region before entering the mouth.

The oesophageal valve is not formed by a folding of the fore intestine but by special elongated cells. This is unusual since an oesophageal value is usually formed by the fore intestine extending into the mid-intestine, then folding back upon itself, outward, to the anterior edge of the mid intestine. An oesophageal valve formed by elongated cells has the shape of one formed by a fold of the fore intestine and no doubt is just as efficient.

The mid-intestine or stomach is that part of the alimentary canal posterior to the oesophageal valve and anterior to the entrance of the Malpighian tubules. There is no cuticular covering of the digestive epithelium in the mid-intestine. The cells of the mid-intestine are rather small and flattened in the region of the oesophageal valve, but posteriorly they become more columnar and irregular in size and shape. The first section of the stomach is unusual in that the portion lined with digestive epithelium is very small in relation to the size of the pouch. The capacity of this section of the stomach is reduced by crowding, caused by the folding of the stomach wall around portions of the hind-intestine and mid-intestine and Malpighian tubes. Plate II, Figure 6, shows a longitudinal section through the oesophagus, and anterior and posterior diverticula. This section shows that a large portion of the anterior diverticulum is occupied by the many loops of the Malpighian tubes and the mid-intestine and hind-intestine between folds of the diverticular wall. The posterior diverticulum shown in Figure 6 has also folded over a portion of the stomach and Malpighian tubes. This enclosing, by folding of the posterior diverticulum, occurs when these parts cross the diverticulum as shown in Plate I, Figure 1. The intestine and Malpighian tubes are not usually folded under by this section. It should be noted that the loops of the intestine and Malpighian tubes do not enter the stomach but are only under folds of the diverticular walls and are sealed over with connective tissue. This enfolding of the alimentary canal by the diverticulum is present in first-instar nymphs and evidently first occurs in the embyronic development.

The cells of the anterior diverticulum are large, irregular in size, and columnar in shape. The same type of cell continues throughout the stomach, but with variations in size. The largest epithelial cells occur in the posterior diverticulum and the smallest cells occur posterior to the stomach constriction. The constriction of the stomach shown in Plate I, Figure 1, and Plate II, Figure 13, located at the posterior end of the fifth abdominal segment is not a valve. Longitudinal and cross sections were made through the constriction in the stomach, and these failed to reveal any trace of a valve. (Fig. 13).

Posterior to the constriction the gut is always full of large yellow bodies that have the consistency of cheese. These bodies have large nuclei and in the cytoplasm are transparent particles. Kershaw (5) has described a similar body found in the alimentary canal of *Tomaspis saccharina* Dist., a cercopid. He had the contents of two nymphal posterior guts analyzed and reports the granules to be amorphous insoluble calcium phosphate and to constitute 80 per cent of the content of the gut.

The function of these yellow bodies in the alimentary canal is not known. Their color is undoubtedly due to bacteria, since four pure strains which produced yellow colonies on beef agar have been isolated on numerous occasions from smears taken from one of these macerated bodies. A further study is planned of the fauna of the alimentary canal of this spittle bug and this should give some interesting results.

The ascending portion of the gut in the folds of the anterior diverticulum is stomach to the point of entrance of the Malpighian tubes, (Plate I, fig 2). The large digestive epithelial cells disappear in the alimentary canal at this point, and the intestine posterior to this point is lined with chitin, which is definite proof that the division of stomach and hind intestine has been reached. A slight enlargement at this point may indicate a pyloric valve, although no trace was found of one in sections from this region.

The cells of the rectum are relatively small and uniform throughout this portion of the canal, and there is very little variation in the thickness of the chitinous lining. (See Figures 13 and 14.)

## Source of Spittle or Froth.

The source of the small white frothy masses noticed on many plants in the spring of the year has been explained in many and various ways. It was first written by Isidorous, cited by Gruner (3), in the sixth century that these white spittle masses were spit of the cuckoo bird and that small insects were spontaneously generated from it. It was also thought that certain plants secreted the spittle mass. According to Gruner (3), Bock in 1546 made a list of the plants that produced spittle. There are even sections of this country today where the people believe these spittle masses are the spit of snakes or cuckoos. These explanations of the source of the spittle, along with many other such theories, we know to be incorrect.

There are also several other more modern theories which have been advanced in explanation of the production of the spittle. It has been thought that the spittle is the production of salivary glands, or of special glands located in the abdomen, such as the Glands of Batelli, and the Malpighian tubules.

This study to determine the source of the spittle has consisted of field observations, laboratory experiments, and study of the histological structure.

The field observations on habits of the spittle-bug nymphs showed two things of interest; first, that all cercopid nymphs observed always elevate the posterior end of the abdomen, and, second, that they occasionally extend and retract the posterior segments in a telescoping fashion. This position of the abdomen is maintained at all times but the movement described takes place at short intervals when the nymph is covered with the clear fluid before bubbles are formed. These two habits are important in the formation of the spittle. A spittle-bug nymph removed from its covering of spittle to dry blotting paper will lose its external covering of fluid. When this nymph is replaced on a plant it soon locates a favorable spot for feeding, and inserts its beak into the plant tissue. Observation records show that the nymph moves its middle and posterior pairs of legs at intervals while feeding. This movement of the legs has been described by Guilbeau (4) as a means used by the nymph to mix the spittle as secreted. This habit of moving the legs when feeding is evidently not exclusively a function necessary to the production of spittle, since it has been observed as common to many Hemiptera and is not restricted to cercopids. The nymph increases in size as it feeds, and after feeding from 1 to 2 minutes it excretes a clear fluid from the anus. In from 5 to 12 minutes the nymph is completely covered with the fluid. The position of the tip of the abdomen when the fluid is excreted, causes the fluid to flood the dorsal surface of the abdomen and run off the sides of the body. When the nymph is covered with clear fluid the tip of the abdomen is extended outside the fluid. While outside the fluid, the posterior lateral folds are opened to allow entry of air, then closed as the abdomen is retracted into the fluid. The body of the nymph is then contracted and a bubble of air is released into the fluid. This process is performed repeatedly until the clear fluid becomes a white frothy mass or spittle. In the method of forming the spittle I agree with Morse (7) but do not agree with him that the anal appendages serve as gills when the nymph is covered with spittle.

A study of the ventral external structure of the spittle-bug nymphs shows how air is taken and released. The sternal body wall is almost a flat surface, but the terga and pleura are greatly extended and when folded under the abdomen, meet and form a closed tube, or air space, for the entire length of the abdomen. It is evident that this tube is filled with air when the tip of the abdomen is thrust outside the fluid, and that when the abdomen is retracted under the fluid air is released and forms the bubbles. This air reservoir also has the function of transmitting air to the spiracles for use by the insect, since the spiracles are located in this region. The location of the spiracles and existence of the air reservoir explain how the nymphs breathe even though submerged in the spittle.

We have seen from observations that the clear fluid of which the spittle is formed is excreted at the anus.

The detailed histological study disproved several of the theories as to the source of the spittle. It is evident that the salivary glands do not directly secrete the fluid for the spittle, since the secretion from these glands is carried by ducts to the mouth. No special spittle glands were found in any part of the body of the species studied. The glands of Batelli (1) are described as being located on the seventh and eighth abdominal segments and to secrete a semi-solid material through the chitin of the seventh and eighth somites which is mixed with the excretion from the anus by use of the second and third pairs of legs to form the spittle. These glands or openings were not found in this study.

The theory that the anterior smooth portion of the Malpighian tubes secretes the fluid with which the spittle is formed can not be disproved at this time; however, this theory does not appear logical. The anterior smooth portion of the Malpighian tubes has very thin walls composed of small cells. This structure is not compatible with the fact that spittle bugs secrete a relatively large quantity of clear fluid in a short time. Also it has been proved experimentally that a spittle-bug nymph will die without forming spittle unless it can find a plant on which to feed. If the spittle were a secretion, the glands should possess enough stored fluid to produce at least a small quantity of spittle without feeding. This is not the case since many nymphs have been held under observation, and they have always fed for at least 1 minute before excreting any fluid. A nymph that is removed from a spittle mass and then replaced on a plant will enter the first spittle mass encountered, evidently seeking protection before food. A nymph placed on a semidry, cut plant is able to insert its proboscis, but owing to the dryness of the plant is unable to secure any sap. Under these conditions a nymph does not excrete any fluid for spittle which would act as a protective covering. This indicates that the nymphs require food before any liquid is excreted for spittle. The fact that no special glands with anal openings were found in this study, and that other investigators have observed that the clear liquid is excreted at the anus, indicates that the clear fluid from which the spittle is formed is the normal excretion from the alimentary canal. The excretion would include secretions and excretions from the different cells and glands throughout the alimentary canal. It is evident that the quantity of excretion is determined by the rate of feeding or that the spittle-bug nymph is able to control the rate of flow of sap through the alimentary canal.

Licent (6) found by analysis that spittle consisted of 99.44 per cent water, 0.14 per cent organic matter, and 0.38 per cent inorganic material and that plant sap consisted of 94.57 per cent water, 3.83 per cent organic material, and 1.61 per cent inorganic material. The results of these analyses are additional proof that spittle is formed from excretion filled with air bubbles.

## LITERATURE CITED.

(1) **Batelli, Andrea.** 1918. Die una particolarita nell' integuments dell Aphrophora spumaria. Monitore, Zool. ital. 11: 30–32. (Original not seen.)

(2) **Gadd, G. G.** 1902. Uber den Bau des Darmkanal bei den Larven von Aphrophora spumaria L. Trav. Soc. Natur. de Petersburg. Zool. et phys. 31: Part 4, 84–95.

(3) **Gruner, Max.** 1901. Biologische untersuchungen an Schaumcikaden. Inaugural Dissertation, Berlin. (Original not seen.)

(4) **Guilbeau, B. H.** 1914. The Origin and Formation of the Froth in Spittle Insects. Amer. Naturalist 42: 783–789; illus. (Bibliography of 21 publications.)

(5) **Kershaw, J. C.** 1914. The Alimentary Canal of a Cercopid. Psyche 21: 65–72, illus.

(6) **Licent, Emile.** 1912. Reserches d' anatomie et de Physiologie Comparees sur le tube digestif des Homopteres superieurs. La Cellule 28, illus. (Good bibliography.)

(7) **Morse, E. S.** 1900. A Bubble Blowing Insect. Pop. Sci. Mon. 57: 23–29, illus.

## EXPLANATION OF PLATES.

### PLATE I.

Fig. 1. Diagrammatic dorsal view showing alimentary canal of nymph of *Philaenus leucophthalmus*.

Fig. 2. Simplified diagrammatic drawing showing ventral view of anterior and posterior diverticulum, showing route of gut and Malpighian tubes, enfolded by anterior diverticulum.

Figs. 3, 4 and 5. Diagrammatic drawing showing entry of stomach in folds of diverticulum.

### PLATE II.

Fig. 6. Longitudinal section through oesophagus, oesophageal valve, anterior and posterior diverticula, showing by dotted line position of diverticula when expanded.

NOTE—Posterior diverticulum has enfolded a portion of stomach and Malpighian tubules.

Fig. 7. Cross-section through anterior and posterior diverticula before they join.

Fig. 8. Cross-section through anterior and posterior diverticula showing constriction where they join. This section is posterior to Figure 7.

Fig. 9. Cross-section through oesophagus.

Fig. 10. Cross-section through oesophagus posterior to Figure 9.

Fig. 11. Cross-section through upper salivary gland.

Fig. 12. Cross-section through lower salivary gland.

Fig. 13. Longitudinal section through stomach showing constriction and presence of yellow bodies posterior to constriction.

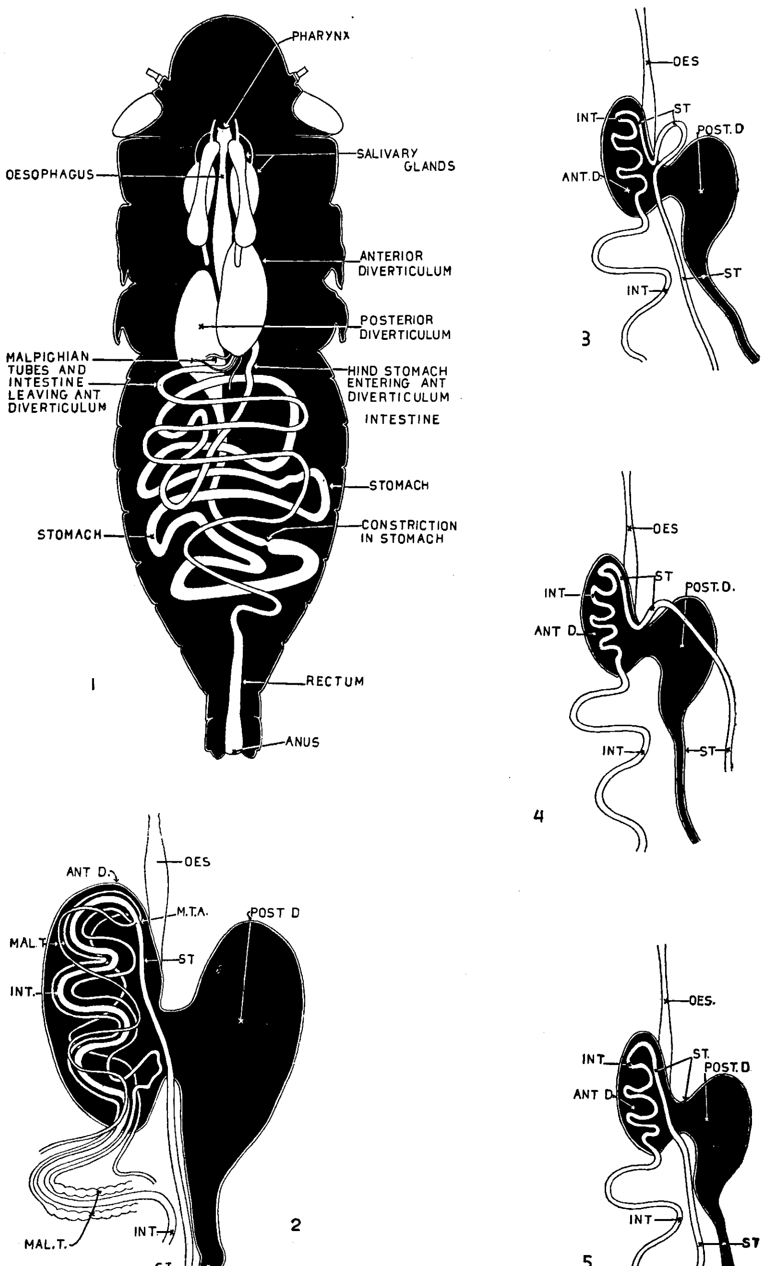
Fig. 14. Cross-section through rectum.

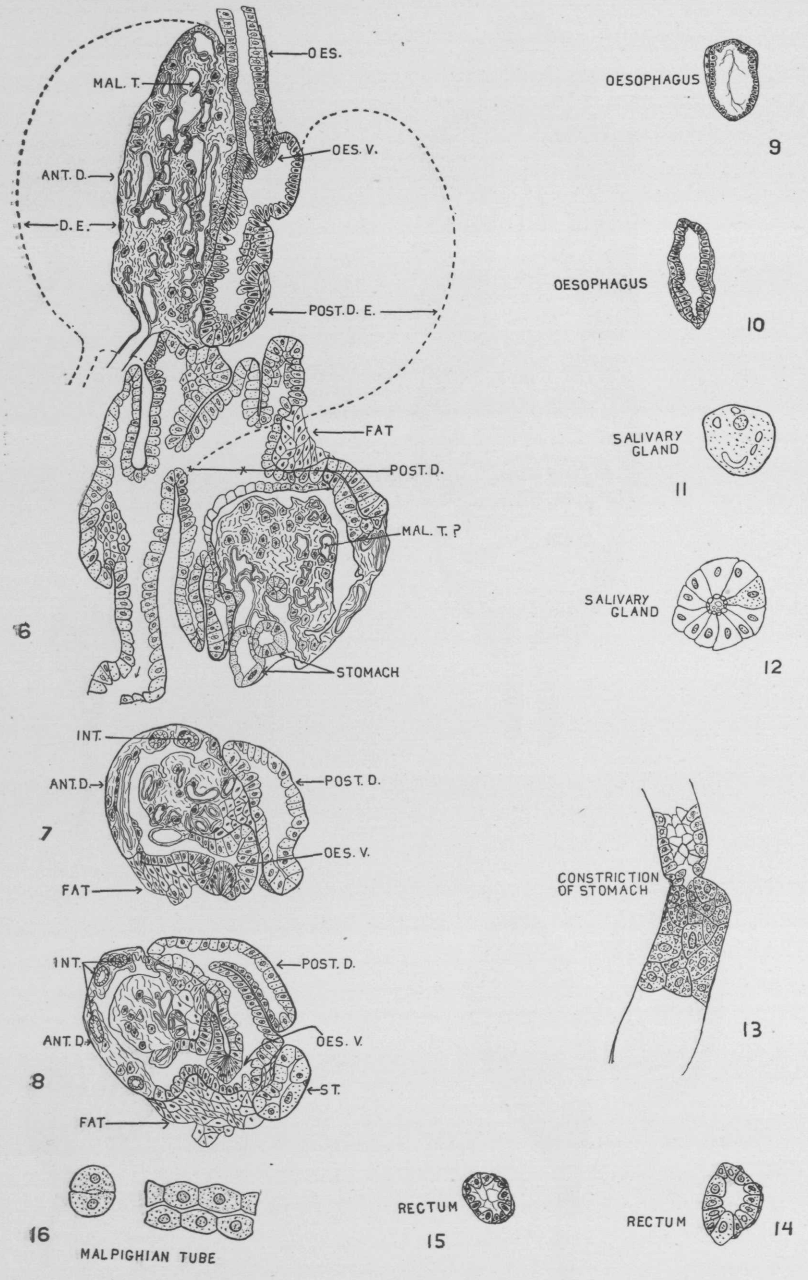
Fig. 15. Cross-section through rectum posterior to Figure 14.

Fig. 16. Cross and longitudinal section through beaded part of Malpighian tubule.

## EXPLANATION OF ABBREVIATIONS.

Ant. D......Anterior diverticulum.
D. E........Diverticulum expanded.
Fat.........Fat tissue.
Int..........Intestine.
Mal. T......Malpighian tubes.
M. T. A.....Malpighian tubes attachment.
Oes.........Oesophagus.
Oes. V......Oesophageal valve.
Post D......Posterior diverticulum.
Post. D. E..Posterior diverticulum expanded.
St..........Stomach.


PHARYNX
OESOPHAGUS
SALIVARY GLANDS
ANTERIOR DIVERTICULUM
POSTERIOR DIVERTICULUM
MALPIGHIAN TUBES AND INTESTINE LEAVING ANT DIVERTICULUM
HIND STOMACH ENTERING ANT DIVERTICULUM
INTESTINE
STOMACH
STOMACH
CONSTRICTION IN STOMACH
RECTUM
ANUS
1
ANT D.
OES
M.T.A.
POST D
MAL.T.
ST
INT.
MAL.T.
INT.
ST.
2
OES
INT.
ST
POST. D
ANT. D.
ST
INT.
3
OES
INT.
ST
POST. D.
ANT D.
INT.
ST
4
OES.
INT.
ST.
POST. D
ANT D.
INT.
ST
5


OES.
MAL. T.
OES. V.
ANT. D.
D. E.
POST. D. E.
FAT
POST. D.
MAL. T. ?
STOMACH
6
OESOPHAGUS
9
OESOPHAGUS
10
SALIVARY GLAND
11
SALIVARY GLAND
12
INT.
ANT. D.
POST. D.
OES. V.
FAT
7
INT.
POST. D.
ANT. D.
OES. V.
ST.
FAT
8
CONSTRICTION OF STOMACH
13
16
MALPIGHIAN TUBE
RECTUM
15
RECTUM
14